

Coping with the commute: Behavioural responses to wind conditions in a foraging seabird

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ABSTRACT

Movement is a necessary yet energetically expensive process for motile animals. Yet how individuals modify their behaviour to take advantage of environmental conditions and hence optimise energetic costs during movement remains poorly understood. This is especially true for animals that move through environments where they cannot easily be observed. We examined the behaviour during commuting flights of black-legged kittiwakes *Rissa tridactyla* breeding on Middleton Island, Alaska in relation to wind conditions they face. By simultaneously deploying GPS and accelerometer devices on incubating birds we were able to quantify the timing, destination, course and speed of flights during commutes to foraging patches, as well as how wing beat frequency and strength relate to flight speeds. We found that kittiwakes did not preferentially fly in certain wind conditions. However, once in the air they exhibited plasticity through modulation of effort by increasing air speed (the speed at which they fly relative to the wind) when travelling into headwinds and decreasing their air speed when flying with tailwinds. Moreover, we identified a biomechanical link behind this behaviour: that to achieve these changes in flight speeds, kittiwakes altered their wing beat strength, but not wing beat frequency. Using this information, we demonstrate that the cost of flying into a headwind outweighs the energy saving benefit of flying with a tailwind of equivalent speed; therefore, exploiting a tailwind when commuting to a foraging patch would not be beneficial if having to return in the same direction with the same conditions. Our findings suggest that extrinsic factors, such as prey availability, have a more influential role in determining when and where kittiwakes fly during foraging trips than do wind conditions. However, once flying, kittiwakes exhibit behavioural plasticity to minimise transport costs.

Keywords: Accelerometer, behavioural adaptation, flight behaviour, GPS, maximum range speed, seabird, wind

INTRODUCTION

Energetic costs arising from locomotion can account for a large proportion of an animal's energy expenditure (Birt-Friesen et al. 1989). Although the way in which animals move and the energetic costs accrued through movement are greatly influenced by their morphology (Aerts et al. 2000, Dial 2003), many species exhibit behavioural adaptations to reduce their energy costs of transport. For example, great hammerhead sharks *Sphyrna mokarran* swim on their sides to exploit the greater amount of lift their abnormally large dorsal fins can then generate (Payne et al. 2016), orangutans *Pongo abelii* sway branches to bridge gaps in the forest canopy that they otherwise must circumvent with a route-extending detour (Halsey et al. 2016, Thorpe et al. 2007) and many ungulates nod in phase with their leg movements, minimising the energy required to carry their head and neck (Loscher et al. 2016). Such widespread and numerous behaviours all serve to reduce the energy cost of transport, suggesting that minimising this cost is beneficial (Halsey 2016).

Many seabirds forage for extended periods of time at sea, often facing the challenge of commuting between patches of accessible prey. Some seabird species are exemplars of exploiting the ocean environment in a way that minimises transport costs from commuting. Soaring seabirds with low wing loading, such as albatrosses and frigate birds, can exploit the windscares they encounter to travel vast distances while expending very little energy (Shaffer 2011). This shapes not just the way in which they fly, but also where they choose to fly (Weimerskirch et al. 2016, Weimerskirch et al. 2000, Weimerskirch et al. 2012). However, at the other extreme, species such as auks and shags, which have a high wing loading and need to continuously flap to stay in flight, face exceptionally high flight costs (Elliott et al. 2013a, Elliott et al. 2013b) that can be exacerbated by strong winds (Elliott et al. 2014). This raises the question as to whether seabirds that employ flapping flight exhibit behaviours that limit the considerable energy costs their flying can entail. For example, do they adapt their flight timings and destinations in response to the wind conditions they face (as has been recorded in bird species during migratory flights (Åkesson and Hedenström 2000, Liechti 2006, Mateos-Rodríguez and Bruderer 2012)), or, once in the air, do they adjust their flight behaviour to optimise efficiency?

During the breeding season, seabirds are central-place foragers and not only face the direct energetic costs of raising young (Regular et al. 2014), but also the time and energy costs of frequently commuting

between their breeding site and foraging grounds. How individuals respond to environmental conditions such as prevailing wind conditions during this period of high energy demand, hampered by time-constrained movement (Gales and Green 1990, Shaffer 2004), is poorly understood for most seabird species. This is largely due to flight being particularly difficult to study in-situ (Elliott 2016, Guigueno et al. 2019). Theoretical approaches to understanding behaviour during flight have led to aerodynamic models that predict how individuals might fly to minimise their transport energy costs (Pennycuick 2008). Two different strategies have been proposed to explain how continuously flapping birds might adjust their flight: maximum range speed and minimum power speed. Maximum range speed is the air speed that covers the greatest air distance per unit of energy, while minimum power speed is the air speed corresponding to the lowest required rate of energy expenditure to stay in flight. Minimum power speed leads to the longest time spent flying without needing to refuel, yet does not result in the greatest distance travelled before needing to refuel (Pennycuick 2008). According to optimal flight theory, minimum power speed should not be affected by wind speed while maximum range speed is predicted to increase when flying into headwinds (Hedenström and Ålerstam 1995, Hedenström et al. 2002). Changes in flight speed are achieved through changes in wing beat patterns, yet how specific wing beat patterns relate to changes in flight speed during flight in the wild are not well understood. The study of flight biomechanics in the wild is largely in its infancy, with much of our knowledge to date being derived from wind tunnel experiments. Although valuable, the artificial environment introduces limitations that may alter measures of flight behaviour (Van Walsum et al. 2019). By linking changes in flight speed to the flight biomechanics underpinning them, as recorded in-situ, a more complete understanding of flight behaviour in the wild and its impacts on an individual's energetics can be obtained.

Biologging devices can shed light on the movement choices and flight behaviours of birds at sea (Cooke et al. 2004), allowing us to investigate whether they do indeed optimise their flight in line with theoretical models. To date, studies using biologging devices to examine the influence of wind on seabird flight have tended to focus on the extreme soarers such as frigate birds and albatrosses (e.g. (Wakefield et al. 2009, Weimerskirch et al. 2016) or, at the other end of the spectrum, species with high wing loading and obligate flapping flight, such as shags (Kogure et al. 2016) and auks (Elliot et al. 2013a) . Less is understood about how birds with more flexible flight behaviours, which represent the majority of seabirds, either utilise and/or are constrained by the wind conditions they encounter. Furthermore, even

less is known about how such birds might achieve changes in flight speeds through nuances in flapping behaviour. In the present study we investigate the flight behaviour of the black-legged kittiwake *Rissa tridactyla* (hereafter kittiwake), during the breeding season. The kittiwake is a medium-sized species of gull which feeds at, or slightly-below, the sea surface. Being incapable of actively pursuing prey through the water column, flight is its single mode of locomotion when travelling at sea. Kittiwakes have a flap-glide style of flight, though predominate with flapping flight (Birt-Friesen et al. 1989), with flight costs accounting for a large proportion of their daily energy expenditure during the breeding season (Collins et al. 2016). We elucidate how breeding kittiwakes respond to wind conditions during commuting flights that form part of their foraging trips, and predict that this species should expend its energy stores on foraging excursions judiciously. By combining simultaneous GPS and acceleration data with measures of wind speed and direction, we examine kittiwake flight behaviours that operate at two spatio-temporal scales. At the broader scale we ask the question: Does wind influence destination and timing of commuting flights? At a finer scale we ask the question: Do kittiwakes alter their flight speeds and wing beat patterns in response to wind conditions? Through linking both flight speeds and wing beat patterns, we aim to shed light on how biomechanics links to bird flight behaviour and consider this in ecological terms. From our measures of flight speed and wingbeat patterns, we address the question: For kittiwakes, what are the energetic implications of flying against headwinds or with tailwinds?

MATERIALS AND METHODS

Data collection

We collected simultaneous GPS and tri-axial accelerometry data from 62 incubating kittiwakes breeding on the radar tower colony on Middleton Island, Alaska (59°27'N, 146°18'W) between May 30 and June 18 2013. Accelerometers (3 g, Axy, Technosmart, Rome, Italy) were set to record at 25 Hz, while GPS loggers (14 g, CatTraQ™, Catnip Technologies, USA) were set to record at 1-minute intervals. Both devices were attached (as a single combined unit) to the central back feathers of kittiwakes using strips of TESA tape. Data was collected from 62 birds, however we used only those which successfully recorded both accelerometry and GPS data simultaneously, and which recorded data until retrieval of the loggers, thus giving a dataset of 47 combined deployments. The mean kittiwake mass at time of deployment was 467 ± 37 g (range 395-540 g). The GPS and accelerometer combined weighed a total of ~ 20 g when packaged, thus accounting for a mean of 4.3% of body mass (range 3.7-5.1%). All activities were approved by the University of Manitoba under the guidelines of the Canadian Council on Animal Care (protocol F11-020), as well as by the US Fish & Wildlife

Service and the Alaska Department of Fish & Game. Devices of an equivalent mass have been shown to reduce the amount of time kittiwakes spend flying, although no effects on longer term performance measures such as reproductive success were detected in the same study (Chivers et al. 2015). The device effect on behaviour needs to be considered when interpreting the results, however instrumented birds still needed to (and indeed did) fly when carrying biologgers and as such we suggest that the overall influence of wind on movement behaviour was likely to remain. A subset of the data collected here has been analysed and interpreted in Elliott et al. 2014, however the much larger sample size presented here (47 birds versus eight) allows us to more fully explore questions around flight, wind and biomechanics in kittiwakes.

We used a weather dataset from the Middleton Island Airport that comprised of wind speed and wind direction recorded within 1 km of the colony at 20 min intervals (<http://cdo.ncdc.noaa.gov/qclcd/QCLCD>). We collated these data from the start time of the first logger dataset to the end of the last. To characterise the overall prevailing wind conditions and to identify if there was an association between time of day and wind conditions, average wind speed and direction per hour of the day were calculated and visualised using the “metvurst” package in R 3.2.1 (R Core Team 2014).

Behavioural assignments

To identify periods of flight and full foraging trips, acceleration data were assigned to three coarse-scale behaviours: “nest attendance”, “on water”, and “flying”. Although finer-scale behaviours such as foraging, preening, and courtship are exhibited by kittiwakes, the amount of time these behaviours take up is relatively little (Jodice et al. 2003). As per Collins et al. 2015, behaviours were assigned using a simple method that categorises different activity types based on readily calculable metrics indicating body orientation or amount of movement. Behaviours were assigned per second of accelerometry data. Behaviours of “nest attendance” and “on water” were assigned depending on the body angle of the bird; periods when the bird was at a lower angle were assigned as “on water”, and periods at which the bird was at a higher body angle were identified as being on land. The body angle thresholds at which these behaviours were separated were specific to each individual. When classified as on land, birds were assumed to be attending their nest, and were thus assigned the behaviour “nest attendance”. Flight was assigned based on the standard deviation of acceleration values in the heave axis, with higher values indicating movement in this channel relating to flight. This method of behavioural classification has been shown to give high accuracy (>95%) of coarse-scale behaviour assignments in kittiwakes (Collins et al. 2015). However, to further enhance the accuracy of this approach, a rule was applied to the data whereby assignments of “on land” could not be assigned when accompanying GPS data indicated that the bird was at sea; likewise when GPS data indicated that the bird was over land an assignment of “on water” could not be made. Foraging trips were defined as a period in which the bird flew from the land, spent time on water, and then returned to the land, with trips varying in duration. Only trips over 30 min were used, to exclude periods when birds might have left the land for reasons other than foraging (such as researcher disturbance or predator avoidance (Collins et al. 2014)). Flight was not separated into flapping or gliding, although kittiwakes flap much more than they glide (Birt-Friesen et al. 1989), as verified by visual examination of the raw heave axis acceleration data.

Spatial analysis

As per (Warwick-Evans et al. 2015) we interpolated GPS tracks to one fix per second using the “adehabitatLT” package (Calenge 2006) in R 3.2.1 (R Core Team 2014) so that it was at the same frequency as, and could therefore be combined with, accelerometry behaviour data. We used the

“geosphere” package in R (Hijmans et al. 2012) to measure the distance between interpolated GPS locations to calculate total distance travelled and maximum distance from the colony.

Kernel density analysis

We used the Geospatial Modelling Environment software (Beyer 2012) to estimate the kernel densities and the 50% kernel home ranges of the birds’ at-sea distributions. Only data relating to when birds were in flight (as indicated by prior behavioural assignments) were included in the distribution density estimates. This analysis therefore reflects foraging destinations and flight directions, rather than areas where the birds may have spent a large amount of time loafing on the water. Cell size was set to 1 km² while the bandwidth was obtained using the plug-in estimator (Wand and Jones 1994) in the “ks” package (Duong 2015) in R.

Flight speeds and direction

GPS data were used to calculate measures of flight speed per second. The ground speed vector V_g (the speed of flight measured from the GPS track) was calculated by dividing measured distance travelled by time taken, while the air speed vector V_a (the speed the bird is flying after accounting for the speed and direction of the wind) was measured by subtracting the wind speed vector V_w from ground speed vector (Kogure et al. 2016):

$$V_a = V_g - V_w$$

Wind data were interpolated between each twenty minute sampling interval and matched to associated GPS data point as measured per second. The wind speed vectors (which we refer to as tailwind speed in our analyses) were calculated by estimating the wind vector in direction of flight parallel to the bird as measured by GPS heading using the “RNCEP” package (Kemp et al. 2012) in R. All speeds were calculated in m s⁻¹. Although ground and air speeds were calculated for all flights, we excluded from our analyses flights relating to periods when the birds were most likely foraging - identified through measures of speed estimated in R and visual inspection of the data in ArcGIS (ESRI, USA, version 10.0) as having high tortuosity and low ground speeds. Foraging was omitted so that we could focus on the influence of wind on commuting flights alone. Flight speeds used in analyses are averages across each flight, with the first and last 50 seconds removed to reduce the influence of changes in speed during take-off and landing.

Flight direction was examined at two scales. To understand the general direction of travel for first and last commuting flights in a foraging trip, the direction between the first (take-off) and last (landing) GPS fixes of these flights were calculated. Whereas to identify if birds preferentially flew with wind assistance when in flight, the angular difference between the direction of flight and wind direction during flight was calculated. Direction of flight was subtracted from wind direction per second during each flight and then averaged across each full flight. By calculating this value per second we account for potential changes in both wind and bird direction during flights. To identify if there was any significant deviation from a uniform distribution of angular differences between flight and wind directions we conducted a Rao's spacing test ($\alpha = 0.05$).

Wing beat parameters

Dominant wing beat frequency was calculated using peak spectral density on Fast-Fourier transformed acceleration values (g) in the heave axis (the dorso-ventrally orientated axis). It was calculated across commuting flights, however the first and last 50 s of each flight was removed due to wing beat frequencies being more variable during take-off and landing (Elliott et al. 2014). Wing beat strength, was assumed to be directly proportional to body movement amplitude (Van Walsum et al. 2019). As per Kogure et al. 2016, wing beat strength was calculated using the Ethographer application (Sakamoto et al. 2009) in IGOR Pro (Wavemetrics inc., USA 2008, Version 6.37). Continuous wavelet transformation was applied to the raw acceleration data in the heave axis (g), and wing beat strength was calculated as the average of absolute amplitude of each waveform every second. As with estimates of wing beat frequency, the values we derived relate to the dominant wing beat strength across each commuting flight period, with the first and last 50 s of each flight removed.

Statistical analysis

All inferential statistical analyses presented relate to values derived across individual flights. Only flights of a duration of more than 5 min were included in the analyses to ensure that the dominant wing beat frequency and dominant wing beat strength measurements were more likely to represent the dominant signal rather than an outlying value from highly variable signals.

A series of generalised linear mixed models (GLMMs) were constructed to test for the influence of wind on various aspects of flight behaviour. GLMMs were constructed for both flight duration and total distance travelled in relation to wind speed and direction. Further GLMMs were then constructed to examine the influence of the wind speed component in the direction of travel (hereafter tailwind speed) on estimated air speeds, reflecting the effort of birds in the face of varying wind directions at different ground speeds across flights. Following (Shamoun-Baranes et al. 2007), and as implemented by (Kogure et al. 2016, Yoda et al. 2012), we also applied a two-dimensional GAM to analyse the relationship between air speed and wind speed during flights. Wind speed was separated into two components - headwind speed and crosswind speed - and was transformed via LOESS transformation (with a maximum span of 80% and 2 degrees of freedom). Analysis was conducted in the “mgcv” package (Wood 2001) in R. This additional analysis was carried out to identify if findings from the GLMMs were likely to be spurious correlations that can arise from analysing wind data with a one-dimensional model (Shamoun-Baranes et al. 2007). We also constructed GLMMs to identify how air speed was related to the dominant wing beat frequency and wing beat strength for individual flights. Due to each kittiwake undertaking numerous flights during the period in which they were measured, individual bird identity was assigned as a random factor in all GLMMs. All GLMMs were constructed with a Gaussian family and a log link due to each response variable conforming to assumptions of normality. GLMMs were constructed using ‘glmmPQL’ from the MASS package (Venables and Ripley 2002) in R. P values below 0.05 were deemed to be statistically significant.

RESULTS

Broad-scale behaviour

Distribution and direction of flights

We detected a total of 107 foraging trips, which included a total of 558 discrete flights with a duration of 5 min or more. Mean foraging trip duration was 4.3 ± 0.4 h ($n=77$), with mean percentage of total time spent in flight throughout a foraging trip being $47.3 \pm 2.5\%$. The mean total distance travelled per foraging trip was 73.3 ± 5.1 km (range 10.7-201.9 km), with the mean maximum distance from the colony being 21.6 ± 1.4 km (range 3.0 – 57.6 km). On average, foraging trips included 5.2 ± 0.5 discrete flights (range 1 – 26) separated by either feeding bouts or periods of resting on the water. In total, 402 of these flights were classified as commuting flights, thus fitting the criteria for subsequent analysis. Mean duration of these flights was 12.1 ± 0.68 min, covering a mean distance of 5.18 ± 0.41 km.

The majority of recorded foraging trips were to the north, or slightly northeast, of the colony (Figure 1). The 50% kernel density estimates for space use when on a foraging trip highlight the importance of the area immediately to the North of Middleton Island (Figure 1). 94% of initial flights headed northwards between $315 - 135^\circ$, whilst 87% of final flights in each foraging trip (i.e. the return trips) headed southwards, between $135-270^\circ$ (Figure 2). The mean angular difference between the first outwards and the last return flight across all foraging trips was $167.8 \pm 4.7^\circ$.

The influence of wind on initiation and direction of flights

Throughout the study period winds tended to come from either a south to south westerly direction ($200-270^\circ$) or from a north-easterly to easterly direction ($40-100^\circ$). Mean wind speed was 4.2 ± 0.1 m s⁻¹ (range=0-11.2 m s⁻¹). There was no diurnal pattern in wind direction or wind speed (Figure 3).

Hourly wind direction weighted by the number of birds equipped during each hour, and thus indicating available wind conditions for study birds to fly in, reflected the dominant wind conditions over the study period, with winds blowing from either a south to westerly direction or a north east to easterly direction (Figure 4a).

Birds showed no clear preference for flying during periods when the wind was blowing from certain directions or at certain speeds. The distribution of wind conditions during: all flights (Figure 4b), the first

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flight of each foraging trip (Figure 4c) and the last flight for each foraging trip (Figure 4d) did not differ from the overall wind conditions during the study period (Figure 4a). Flight duration was not significantly related to either wind direction ($t_{357}=-0.67$, $p=0.503$) or wind speed ($t_{357}=-1.37$, $p=0.172$), however total distance travelled during a flight was significantly greater with lower overall wind speed ($t_{357}=-2.78$, $p=0.006$), but was not significantly related to overall wind direction ($t_{357}=-0.67$, $p=0.503$).

There was no evidence of birds preferentially flying with tail winds when in flight. The angular difference between wind direction and the overall direction the bird flew in during each flight showed no significant deviation from a uniform distribution (Rao's spacing test, $U=136$, $p>0.05$). Wind speed also did not appear to influence the direction the bird was travelling in relation to the wind (Figure 5).

Fine-scale behaviour

The influence of wind on flight speed and behaviour

Wind speed and direction relative to the birds influenced their speed of travel. Air speed significantly decreased with increasing tailwind speed ($t_{378}=-18.57$, $p<0.001$), described as: air speed= $9.69-0.60*\text{tailwind speed}$ (Figure 6a), suggesting that birds invested greater effort in headwinds and less effort in tailwinds. A two-dimensional GAM identified that air speed was significantly related to one or both of the wind components (tailwind and crosswind) in all individuals ($P<0.001$), suggesting the relationship is not due to a spurious correlation.

The resultant ground speed increased significantly with tailwind speed, described as: ground speed= $8.38+0.34*\text{tailwind speed}$ (Figure 6b) ($t_{382}=8.62$, $p<0.001$) but with a lower gradient, highlighting that in strong tailwinds, birds took the opportunity to reduce their flight effort.

Wing beat strength significantly increased with increasing air speed ($t_{378} = 5.23$, $p<0.001$) (Figure 7a). Since air speed increases in head winds, we conclude that wing beat strength is greater in head winds. There was no significant relationship between wing beat frequency and air speed ($t_{378} = 1.41$, $p=0.160$) (Figure 7b). Mean wing beat frequency across all flights for all individuals was 4.07 ± 0.01 Hz (range= $3.57-4.85$).

DISCUSSION

By coupling positional data with body acceleration and wind data we have cast light on the interplay between wind conditions, movement behaviour and the resultant potential energy implications in a commuting seabird. We found that kittiwakes at Middleton Island select the location, timing and course of their commuting flights apparently without consideration of the strength and direction of winds they experienced, although total distance travelled was greater in lower wind speeds. For this population, at least, extrinsic factors other than wind are apparently more important in determining initiation and destination of their flights. Once in flight, however, kittiwakes modulate their flight effort by increasing wing beat strength to increase air speed of flight in the face of headwinds. By linking flight speeds to wing beat measures, we have not only provided evidence for behavioural optimisation through changes in flight speeds but also identified that alteration of wing beat strength is the mechanistic link underlying this behavioural adaptation.

Our finding that kittiwakes exhibited a decreased ground speed and increased air speed in response to headwinds, and vice versa in tailwinds (Figure 6), builds on previous work conducted on kittiwakes at Middleton Island (Elliott et al. 2014) in which a similar feature was identified on a smaller subset of kittiwakes. This influence of prevailing wind conditions on flight speeds has also been recorded in some other seabird species (Kogure et al. 2016, McLaren et al. 2016), supporting the idea that birds adjust their flight air speed towards a ‘maximum range speed’. At this air speed, the greatest air distance is covered per unit of energy expended (Kogure et al. 2016, McLaren et al. 2016, Pennycuik 2008), as opposed to flying at a minimal power speed, whereby individuals would display the lowest required rate of energy expenditure to stay in flight (i.e. being able to fly for longer rather than further). This study adds to the growing body of evidence that flying towards maximum range speed is a common feature of bird flight.

To achieve greater air speed when flying into stronger headwinds the kittiwakes were clearly expending more energy per unit time; their increased effort manifests as an increase in wing beat strength, with no variation in wing beat frequency. In accordance with our findings, adjustment of air speed through moderating wing beat strength has been noted in European shags *Phalacrocorax aristotelis* (Kogure et al. 2016). On the other hand, other species such as bar-headed geese have been recorded to control flight effort and flight speeds through changing both wing beat frequency and strength (Bishop et al. 2015,

Schmaljohann and Liechti 2009). In Harris's Hawks *Parabuteo unicinctus*, wingbeat frequency was found to be linked to climb power during ascending flights but left a lot of variation unexplained, indicating that other changes in wing kinematics may be playing an important role (Van Walsum et al. 2019). In Western Sandpipers *Calidris mauri* and Cockatiels *Nymphicus hollandicus*, wingbeat frequency declined with flight speed in a wind tunnel, while lowest wingbeat frequency was recorded at intermediate speed in teals *Anas crecca* and Thrush nightingales *Luscinia luscinia* (Pennycuick et al. 1996, Hendrick et al. 2003, Maggini et al. 2017). Outside of avian flight, wingbeat frequency of straw-coloured fruit bats *Eidolon helvum*, is not modified with changes in speed, again suggesting other wingbeat kinematics may be more important (O'Mara et al. 2019). Across a wide variety of birds and bats, flight muscle efficiency decreases with forward speed (Guigueno et al. 2019), implying that any change in wingbeat frequency leads to inefficiencies in conversion to mechanical work. Ultimately, the limited evidence available to date suggests that different species control their flight effort through varying nuances of wing movement.

With a simple model we tested whether there is a benefit to exploiting tailwinds while undertaking directed flight to and from a foraging destination. Flight costs tend to be asymmetrical, whereby the costs of flying into a headwind outweigh the benefits of flying with the equivalent tailwind (Raymond et al. 2010). By calculating the time required to cover a set distance of 5 km under varying wind speeds using the flight speeds we calculated ($\text{ground speed [m/s]} = 8.38 + 0.34 * \text{tailwind speed [m/s]}$) (Figure 6), we can show empirically that headwinds of a certain speed are more unfavourable than an equivalent tail wind speed is favourable. This appears to be the result of kittiwakes taking the opportunity to substantially reduce air speed with strong tailwinds (Figure 6). The asymmetrical shape of the relationship between time taken to cover 5 km and tailwind speed indicates that it takes an increasing amount of time to cover a given distance as tailwinds become headwinds (Figure 8). Furthermore, our analysis of wing beat patterns shows that at higher airspeeds, which tend to be observed when flying into headwinds, not only will kittiwakes be flying for longer, but they will be flapping with a greater wing beat strength; thus they are expending more energy both per unit time and over an extended duration.

In our study, persistent wind conditions coupled with relatively short foraging trips in which individuals typically return to the colony from the direction in which they headed out (average difference between

first outwards flight and last return flight = $167.8 \pm 4.7^\circ$; Figure 2), meant that individuals waiting to exploit seemingly favourable tailwinds would not have gained an energetic advantage as the return flight would have likely been into a more energetically unfavourable headwind. This could well explain why we did not observe kittiwakes displaying a preference for initiating commuting flights in either direction to either the strength or direction of wind conditions (Figures 4b-4d). Conversely, there has been some indication that soaring seabirds such as fulmars leave their nests to forage more frequently during stronger winds, when they would benefit from wind assistance (Furness and Bryant 1996). This contrast to the kittiwakes make sense as fulmars employ a soaring style of flight as opposed to the predominantly flapping flight employed by kittiwakes. However, kittiwakes flying in lower wind speeds travelled larger total distances. This could give some advantages as it would enable them to move more rapidly between foraging patches (Weimerskirch et al. 2012) and hence possibly allow more time to be spent foraging.

In addition to not initiating flights to exploit tailwinds, we also identified that when in flight, the kittiwakes did not adjust their direction of flight in relation to the wind (Figure 5). This is in contrast to species such as albatrosses and red-footed boobies, which show behavioural adjustment of flight paths to ensure they minimise the proportion of time they fly into headwinds (Wakefield et al. 2009, Weimerskirch et al. 2005). Possibly, the wind conditions experienced by kittiwakes at Middleton Island do not typically reach sufficient strength to either blow them off course or influence their decisions about where to fly. The wind conditions during the study period did not consist of prolonged periods of high winds (Figures 3 and 4); average wind speed over the study period was $4.2 \pm 0.1 \text{ m s}^{-1}$. This is similar to the average wind speeds across the full breeding period, (between March and September), which averaged $4.8 \pm 2.8 \text{ m s}^{-1}$. In a study on breeding kittiwakes across two contrasting islands, wind speed was a deterministic factor in initiation and location of foraging flights in one of the colonies, but not the other (Christensen-Dalsgaard et al. 2018). It seems that the nuanced interplay between intrinsic and extrinsic factors are likely to influence the importance of wind conditions on foraging behaviour between different colonies. The wind conditions experienced by kittiwakes on Middleton Island in this study were quite consistent - examining how they respond to more variable wind conditions could help identify at which point wind might play a more deterministic role in influencing timing and direction of commuting flights. It is also a possibility that by measuring wind conditions at a coarse scale at one fixed point, we did not fully capture the diversity in wind conditions the kittiwakes in our study faced when out at sea.

This is unlikely to impact our findings relating to flights when departing the colony, near the colony, or returning from foraging trips, however finer scale wind information better matched to that gathered from the birds could allow further confidence in our findings.

Not only did the kittiwakes demonstrate great consistency in flight direction but also in foraging destination, the latter quite possibly explaining the former (Figures 1 & 2). This suggests they were exploiting a reliable food source. As we do not have prey density data for the area surrounding the study colony we cannot confirm this supposition. However, the association of foraging destination with areas of high prey availability has been demonstrated in many seabird species (Burke and Montevecchi 2009, Fauchald and Erikstad 2002, Raymond et al. 2010, Weimerskirch 2007). The consistency of foraging destination, absence of preference for flying out to that destination during favourable wind conditions, and the lack of adjustment of flight course in response to wind speed and direction suggest that wind was not a deterministic extrinsic factor shaping the commuting flight behaviour of kittiwakes at Middleton Island during the study period. It is likely that prey availability, or perhaps time constraints requiring kittiwakes to reach prey quickly, superseded wind speed and direction in determining the broader-scale features of their commuting flights.

Conclusion

Middleton Island kittiwakes seem unperturbed by the wind conditions they experience when commuting to and from foraging patches. Perhaps the additional energy costs of unfavourable winds are negligible or unimportant to them, or perhaps waiting for better conditions is outweighed by the time lost to not feeding at reliable foraging sites. Another possibility is that persistent winds and relatively short foraging trips mean the same wind conditions will be experienced both on the outward and return journeys, nullifying the value of tailwinds on one leg of the trip or the other. However, once in flight the birds respond to wind conditions by adjusting the pattern of their wing beats apparently to take advantage of tailwinds and minimise the impact of headwinds, thus optimising the speeds at which they fly in terms of minimising the energy they expend.

REFERENCES

- Aerts, P., Van Damme, R., Vanhooydonck, B., Zaaf, A. and Herrel, A. 2000. Lizard locomotion: how morphology meets ecology. – *Neth J Zool* 50: 261-277.
- Åkesson, S. and Hedenström, A. 2000. Wind selectivity of migratory flight departures in birds. – *Behav Ecol Sociobiol* 47: 140-144.
- Beyer, H. 2012. Geospatial Modelling Environment (Version 0.7. 2.1).(software); 2012. – URL: <http://www.spatial ecology.com/gme>.
- Birt-Friesen, V., Montevecchi, W., Cairns, D. and Macko, S. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. – *Ecology* 70: 357-367.
- Bishop, C. M., Spivey, R. J., Hawkes, L. A., Batbayar, N., Chua, B., Frappell, P. B., Milsom, W. K., Natsagdorj, T., Newman, S. H. and Scott, G. R. 2015. The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. – *Science* 347: 250-254.
- Burke, C. and Montevecchi, W. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. – *J Zool* 278: 354-361.
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. – *Ecol Model* 197: 516-519.
- Chivers, L. S., Hatch, S. A. and Elliott, K. H. 2015. Accelerometry reveals an impact of short-term tagging on seabird activity budgets. – *Condor* 118: 159-168.
- Christensen-Dalsgaard, S., May, R. and Lorentsen, S. H. 2018. Taking a trip to the shelf: Behavioral decisions are mediated by the proximity to foraging habitats in the black-legged kittiwake. – *Ecol Evol* 8: 866-878.
- Collins, P. M., Green, J. A., Dodd, S., Shaw, P. J. and Halsey, L. G. 2014. Predation of Black-legged Kittiwake chicks *Rissa tridactyla* by a Peregrine Falcon *Falco peregrinus*: insights from time-lapse Cameras. – *Wilson J Ornithol* 126: 158-161.
- Collins, P. M., Green, J. A., Warwick-Evans, V., Dodd, S., Shaw, P. J., Arnould, J. P. and Halsey, L. G. 2015. Interpreting behaviors from accelerometry: a method combining simplicity and objectivity. – *Ecol Evol* 5: 4642-4654.
- Collins, P. M., Halsey, L. G., Arnould, J. P., Shaw, P. J., Dodd, S. and Green, J. A. 2016. Energetic consequences of time-activity budgets for a breeding seabird. – *J Zool* 300: 153-162.

- Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. 2004. Biotelemetry: a mechanistic approach to ecology. – *Trends Ecol Evol* 19: 334-343.
- Dial, K. P. 2003. Evolution of avian locomotion: correlates of flight style, locomotor modules, nesting biology, body size, development, and the origin of flapping flight. – *Auk* 120: 941-952.
- Duong, T. 2015. ks: Kernel smoothing. – R package version 1.
- Elliott, K. H. 2016. Measurement of flying and diving metabolic rate in wild animals: review and recommendations. – *Comp Biochem Physiol A Mol Integr Physiol* 202: 63-77.
- Elliott, K. H., Chivers, L. S., Bessey, L., Gaston, A. J., Hatch, S. A., Kato, A., Osborne, O., Ropert-Coudert, Y., Speakman, J. R. and Hare, J. F. 2014. Windscares shape seabird instantaneous energy costs but adult behavior buffers impact on offspring. – *Mov Ecol* 2: 17.
- Elliott, K. H., Le Vaillant, M., Kato, A., Speakman, J. R. and Ropert-Coudert, Y. 2013a. Accelerometry predicts daily energy expenditure in a bird with high activity levels. – *Biol Lett* 9: 20120919.
- Elliott, K. H., Ricklefs, R. E., Gaston, A. J., Hatch, S. A., Speakman, J. R. and Davoren, G. K. 2013b. High flight costs, but low dive costs, in auks support the biomechanical hypothesis for flightlessness in penguins. – *Proc Nat Acad Sci USA* 110: 9380-9384.
- Fauchald, P. and Erikstad, K. E. 2002. Scale-dependent predator-prey interactions: the aggregative response of seabirds to prey under variable prey abundance and patchiness. – *Mar Ecol Prog Ser* 231: 279-291.
- Furness, R. W. and Bryant, D. M. 1996. Effect of wind on field metabolic rates of breeding northern fulmars. – *Ecology* 77: 1181-1188.
- Gales, R. and Green, B. 1990. The annual energetics cycle of little penguins (*Eudyptula minor*). – *Ecology* 71: 2297-2312.
- Guigueno, M.F., Shoji, A., Elliott, K.H. and Aris-Brosou, S. 2019. Flight costs in volant vertebrates: A phylogenetically-controlled meta-analysis of birds and bats. – *Comp Biochem Physiol A* 235: 193-201.
- Halsey, L. G. 2016. Terrestrial movement energetics: current knowledge and its application to the optimising animal. – *J Exp Biol* 219: 1424-1431.
- Halsey, L. G., Coward, S. R. and Thorpe, S. K. 2016. Bridging the gap: parkour athletes provide new insights into locomotion energetics of arboreal apes. – *Biol Lett* 12: 20160608.

- Hedenström, A. and Ålerstam, T. 1995. Optimal flight speed of birds. – *Phil Trans R Soc Lond B* 348: 471-487.
- Hedenström, A., Ålerstam, T., Green, M. and Gudmundsson, G. A. 2002. Adaptive variation of airspeed in relation to wind, altitude and climb rate by migrating birds in the Arctic. – *Behav Ecol Sociobiol* 52: 308-317.
- Hedrick, T.L., Tobalske, B.W. and Biewener, A.A., 2003. How cockatiels (*Nymphicus hollandicus*) modulate pectoralis power output across flight speeds. – *J Exp Biol* 206: 1363-1378.
- Hijmans, R. J., Williams, E. and Vennes, C. 2012. Geosphere: spherical trigonometry. – R package version 1: 2-28.
- Jodice, P., Roby, D., Suryan, R., Irons, D., Kaufman, A., Turco, K. and Visser, G. H. 2003. Variation in energy expenditure among black-legged kittiwakes: effects of activity-specific metabolic rates and activity budgets. – *Physiol Biochem Zool* 76: 375-388.
- Kemp, M. U., Van Loon, E. E., Shamoun-Baranes, J. and Bouten, W. 2012. RNCEP: global weather and climate data at your fingertips. – *Methods Ecol Evol* 3: 65-70.
- Kogure, Y., Sato, K., Watanuki, Y., Wanless, S. and Daunt, F. 2016. European shags optimize their flight behavior according to wind conditions. – *J Exp Biol* 219: 311-318.
- Liechti, F. 2006. Birds: blowin'by the wind? – *J Ornithol* 147: 202-211.
- Loscher, D. M., Meyer, F., Kracht, K. and Nyakatura, J. A. 2016. Timing of head movements is consistent with energy minimization in walking ungulates. – *Proc R Soc B* 283: 20161908.
- Maggini, I., Kennedy, L.V., Macmillan, A., Elliott, K.H., Dean, K. and Guglielmo, C.G., 2017. Light oiling of feathers increases flight energy expenditure in a migratory shorebird. – *J Exp Biol* 220: 2372-2379.
- Mateos-Rodríguez, M. and Bruderer, B. 2012. Flight speeds of migrating seabirds in the Strait of Gibraltar and their relation to wind. – *J Ornithol* 153: 881-889.
- McLaren, J. D., Shamoun-Baranes, J., Camphuysen, C. and Bouten, W. 2016. Directed flight and optimal airspeeds: homeward-bound gulls react flexibly to wind yet fly slower than predicted. – *J Avian Biol* 47: 476-490.

- O'Mara, M. T., Scharf, A. K., Fahr, J., Abedi-Lartey, M., Wikelski, M., Dechmann, D. K. N., Safi K. 2019. Overall dynamic body acceleration in straw-colored fruit bats increases in headwinds but not with airspeed. – *Front Ecol Evol* 7:200.
- Payne, N. L., Iosilevskii, G., Barnett, A., Fischer, C., Graham, R. T., Gleiss, A. C. and Watanabe, Y. Y. 2016. Great hammerhead sharks swim on their side to reduce transport costs. – *Nat Comms* 7: 12289.
- Pennycuik, C. J. 2008. Modelling the flying bird – Elsevier.
- Pennycuik, C.J., Klaassen, M., Kvist, A. and Lindström, Å., 1996. Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*) – *J Exp Biol* 199: 2757-2765.
- R Core Team. 2014. R: A language and environment for statistical computing. –
- Raymond, B., Shaffer, S. A., Sokolov, S., Woehler, E. J., Costa, D. P., Einoder, L., Hindell, M., Hosie, G., Pinkerton, M. and Sagar, P. M. 2010. Shearwater foraging in the Southern Ocean: the roles of prey availability and winds. – *PloS one* 5: e10960.
- Regular, P. M., Hedd, A., Montevecchi, W. A., Robertson, G. J., Storey, A. E. and Walsh, C. J. 2014. Why timing is everything: Energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. – *Ecosphere* 5: 1-13.
- Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. 2009. Can ethograms be automatically generated using body acceleration data from free-ranging birds? – *PLoS one* 4: e5379.
- Schmaljohann, H. and Liechti, F. 2009. Adjustments of wingbeat frequency and air speed to air density in free-flying migratory birds. – *J Exp Biol* 212: 3633-3642.
- Shaffer, S. A. 2004. Annual energy budget and food requirements of breeding wandering albatrosses (*Diomedea exulans*). – *Polar Biol* 27: 253-256.
- Shaffer, S. A. 2011. A review of seabird energetics using the doubly labeled water method. – *Comp Biochem Physiol A Mol Integr Physiol* 158: 315-322.
- Shamoun-Baranes, J., Van Loon, E., Liechti, F. and Bouten, W. 2007. Analyzing the effect of wind on flight: pitfalls and solutions. – *J Exp Biol* 210: 82-90.
- Thorpe, S., Crompton, R. and Alexander, R. M. 2007. Orangutans use compliant branches to lower the energetic cost of locomotion. – *Biol Lett* 3: 253-256.

- Van Walsum, T. A., Perna, A., Bishop, C. M., Murn, C. P., Collins, P. M., Wilson, R. P. and Halsey, L. G. 2019. Exploring the relationship between flapping behaviour and accelerometer signal during ascending flight, and a new approach to calibration – *Ibis*. doi:10.1111/ibi.12710
- Venables, V. and Ripley, B. 2002. *Modern Applied Statistics with S*. Chambers SJ, Eddy W, Hardle W, Sheater S, Tierney L. Springer Science, New York, NY, USA.
- Wakefield, E. D., Phillips, R. A., Matthiopoulos, J., Fukuda, A., Higuchi, H., Marshall, G. J. and Trathan, P. N. 2009. Wind field and sex constrain the flight speeds of central-place foraging albatrosses. – *Ecol Monogr* 79: 663-679.
- Wand, M. P. and Jones, M. C. 1994. Multivariate plug-in bandwidth selection. – *Comp Stat* 9: 97-116.
- Warwick-Evans, V., Atkinson, P., Gauvain, R., Robinson, L., Arnould, J. and Green, J. 2015. Time-in-area represents foraging activity in a wide-ranging pelagic forager. – *Mar Ecol Prog Ser* 527: 233-246.
- Weimerskirch, H. 2007. Are seabirds foraging for unpredictable resources? – *Deep Sea Res Part 2 Top Stud Oceanogr* 54: 211-223.
- Weimerskirch, H., Bishop, C., Jeanniard-Du-Dot, T., Prudor, A. and Sachs, G. 2016. Frigate birds track atmospheric conditions over months-long transoceanic flights. – *Science* 353: 74-78.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S. A. and Costa, D. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. – *Proc R Soc Biol Sci Ser B* 267: 1869-1874.
- Weimerskirch, H., Le Corre, M., Ropert-Coudert, Y., Kato, A. and Marsac, F. 2005. The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? – *Proc R Soc Biol Sci Ser B* 272: 53-61.
- Weimerskirch, H., Louzao, M., De Grissac, S. and Delord, K. 2012. Changes in wind pattern alter albatross distribution and life-history traits. – *Science* 335: 211-214.
- Wood, S. N. 2001. mgcv: GAMs and generalized ridge regression for R. – *R news* 1: 20-25.
- Yoda, K., Tajima, T., Sasaki, S., Sato, K. and Niizuma, Y. 2012. Influence of local wind conditions on the flight speed of the great cormorant *Phalacrocorax carbo*. – *Int J Zool* 2012.

Figure Legends

Figure 1. Kernel density for the distribution of all foraging trips across the study period. The intensity of the yellow to red colours indicates density of GPS fixes, with the darker red indicating higher density. The solid black line surrounding the red represents the 50% kernel estimates. Middleton Island is the white shape central to the image, just below the 50% kernel outline.

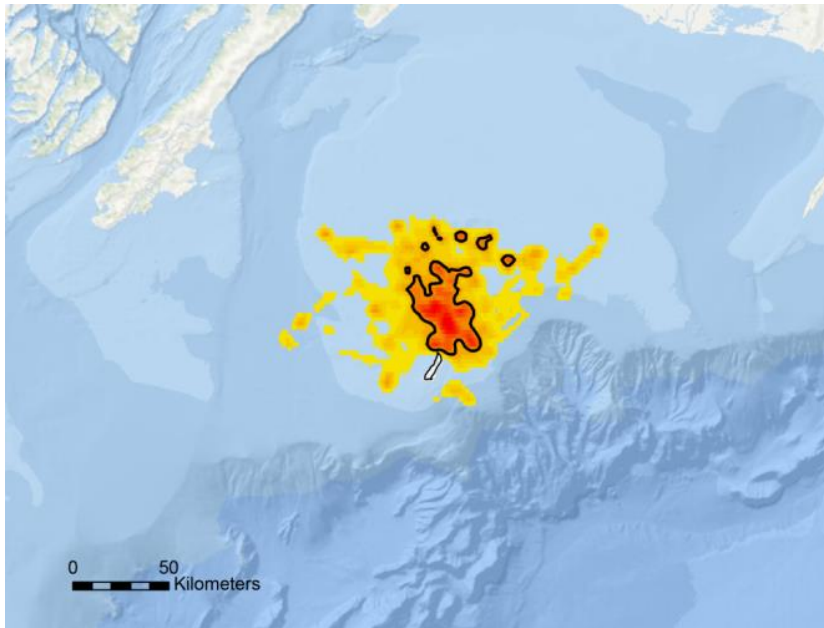


Figure 2. Direction flying towards, and average ground speed of, the first and last flight for each foraging trip.

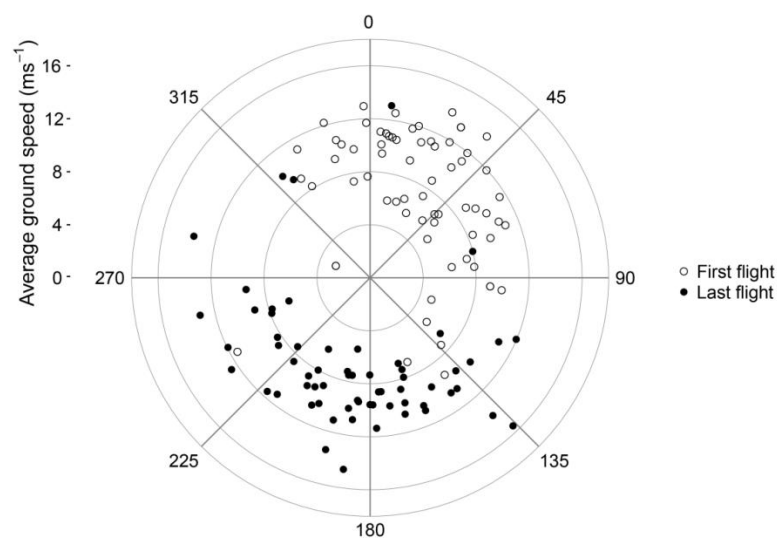


Figure 3. Wind contours for the full duration of the study. The left hand panel indicates hourly frequencies of wind direction, while the panel on the right indicates the distribution of wind speeds per hour. Note that charts indicate the direction wind is coming from.

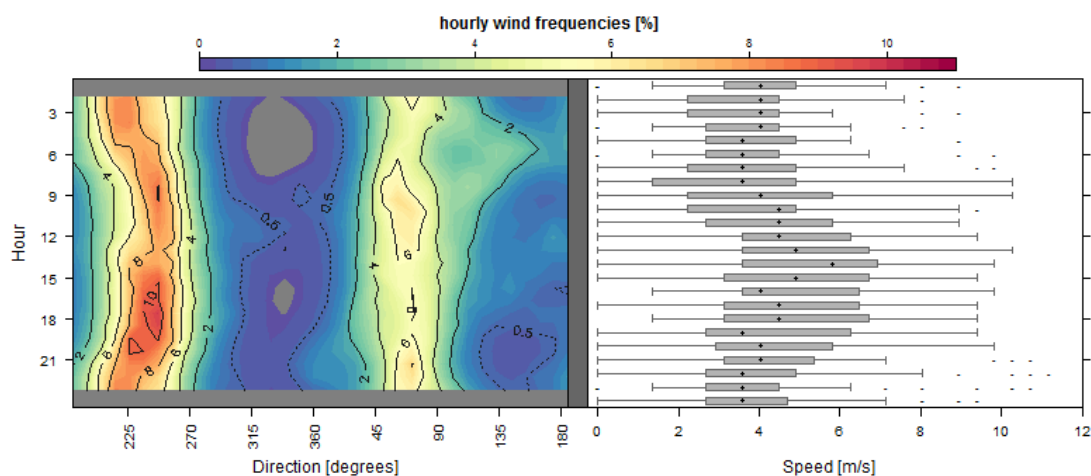


Figure 4 – Wind rose diagrams showing wind direction and strength for: a) the full study period weighted by sample size, b) all flights, c) the first flight from each foraging trip, d) the last flight from each foraging trip. Note that charts indicate the direction wind is coming from.

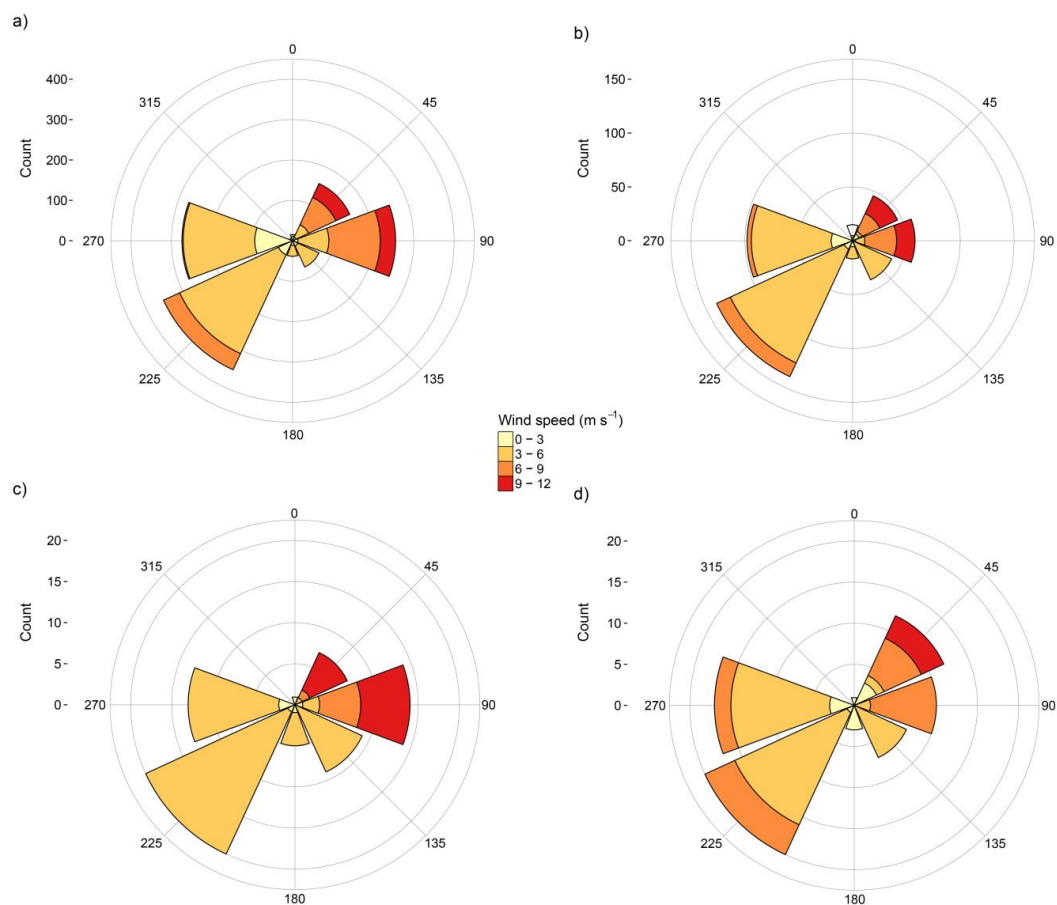


Figure 5 The angular difference between flight direction and wind direction for all flights. Each black dot represents a flight. Values closer to 0 represent birds flying with a tailwind, whereas values of 180 indicate flights in which birds were flying with a headwind.

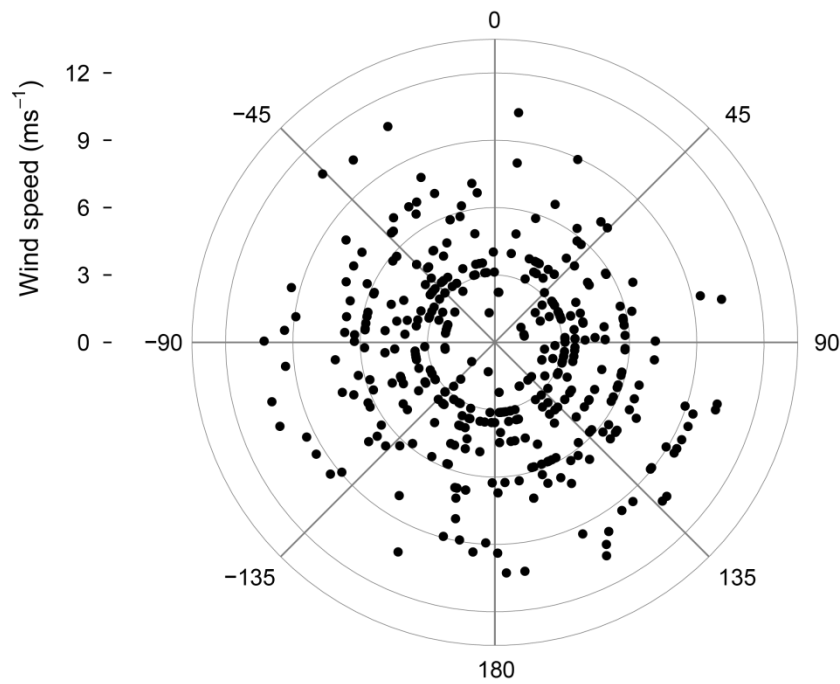


Figure 6 The relationship between tailwind and a) air speed; b) ground speed for all flights over 2 min. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals. Positive values along the x-axis indicate tail winds in relation to the bird, whereas negative values indicate a headwind.

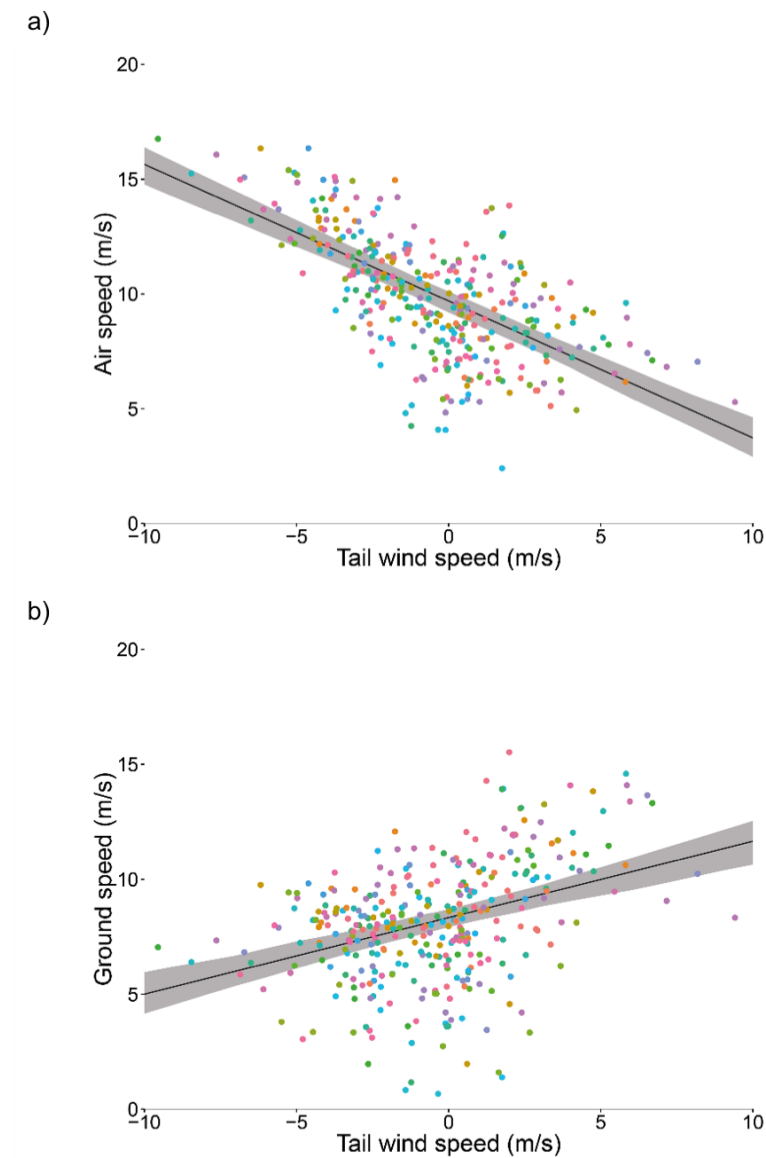


Figure 7 The relationship between air speed and a) wing beat strength and b) wing beat frequency for all commuting flights. Each colour represents an individual bird. The solid line indicates the fixed effect relationship, with the grey ribbon indicating the 95% confidence intervals.

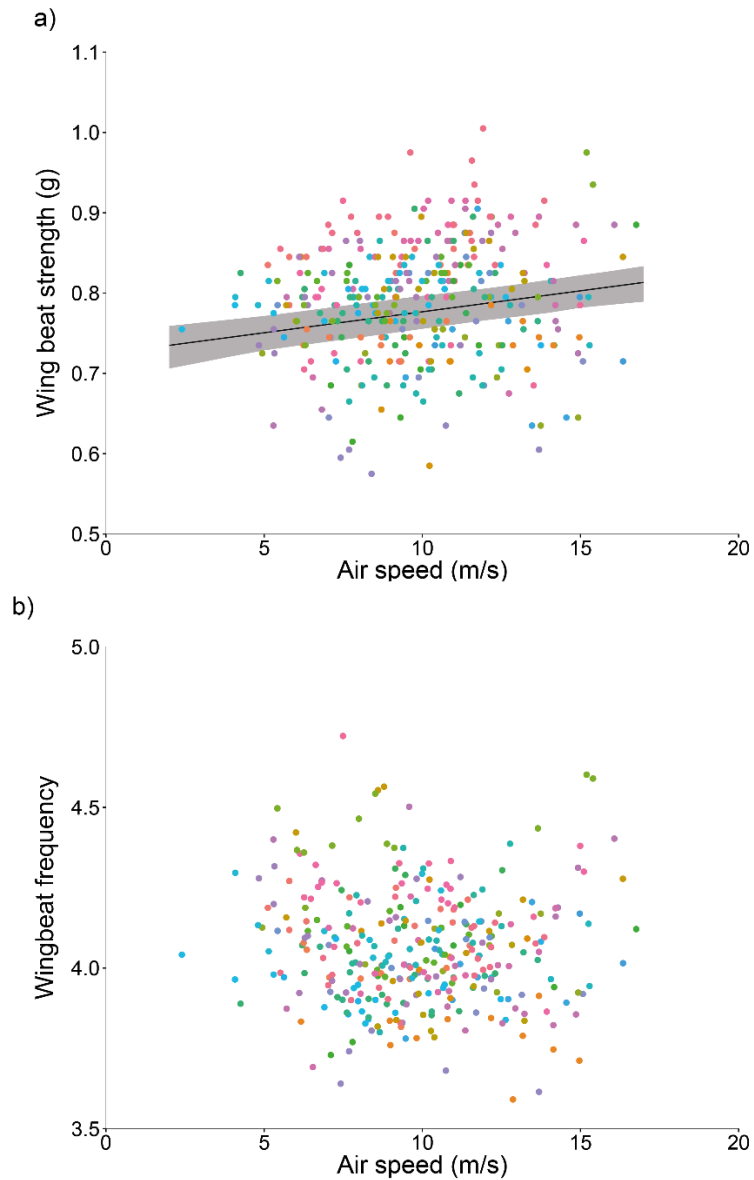


Figure 8 The time taken for kittiwakes from Middleton Island to travel 5 km over the ground in a straight line dependent on wind speed. Positive values along the x-axis indicate tail winds in relation to the bird, whereas negative values indicate a headwind. Times were calculated from the relationship between ground speed and tailwind described in Figure 4.6a (ground speed [m/s] = $8.38 + 0.34 \times \text{tailwind speed [m/s]}$). The curved line is a smoothed conditional mean, calculated using a LOESS estimator.

